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THE BOGS AND BOG FLORA OF THE HURON RIVER VALLEY.

EDGAR NELSON TRANSEAU.

(WITH SIXTEEN FIGURES)

[*Concluded from p. 448.*]

IV. The ecological characteristics of the bog flora and their causes.

The plants occurring in the bog habitat are almost all perennials. In the case of the herbaceous vegetation, the winter is passed by means of subterranean rootstocks. The shrubs are in part evergreen and in part deciduous. The tamaracks and the two birches are deciduous, and the black spruce and pine are evergreen.

Most of the herbaceous and shrubby forms multiply abundantly by vegetative shoots of one form or another. The length of the underground stems of the shrubs is proverbial, but is best appreciated by one who has attempted to dig up one of them entire. In connection with the competition between species for space in the habitat, this is of the greatest importance. A luxuriant growth of *cassandra* furnishes the most favorable situation for the development of sphagnum in this vicinity. Its profuse branching affords a framework for the upbuilding of the sphagnous layer, its shade properties do not interfere with the photosynthetic work of the moss, and it protects it from the drying effects of wind and direct insolation. Where such associations occur, the difficulties presented for the germination for most seeds, and the efficiency with which competition is combated, are evidenced by the fact that among the tree species only the tamarack, spruce, and pine are successful invaders. All of these plants send out adventitious roots from the stems and branches, and so keep pace with the upward development of the moss. The absence of poplars, willows, red maples, and elms in such *undisturbed* situations must be in part attributed to the completeness with which such territory is controlled by the *cassandra*-sphagnum association.

ECOLOGICAL ANATOMY.

Aside from the purely aquatic forms which have received much
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ecological attention, it is of interest to look at the anatomical characteristics of certain of these plants.

Eriophorum virginicum may be taken as a type of this group, and also of the sedge zone vegetation in general. The culm is very slender and erect, leaves flat, and very narrow, perennial by root stocks. *Stem*: epidermis very thick-walled and cuticularized. As development proceeds, certain radial rows of the primary cortex cells have their walls thickened, and served to connect the tissues of the central cylinder with those of the three or four outer layers of hypodermal cells which also become thick-walled. Between these radial groups of cells lysigenic air cavities are formed. *Root*: epidermal cells in part thin-walled and in part secondarily thickened, no definite arrangement of the thick-walled cells apparent; internal structures closely resemble those of the stem; no mycorrhiza present. *Leaf*: outer epidermal cell walls strongly thickened and cuticularized, radial and inner walls less so; lysigenic air spaces traverse the leaf longitudinally; a very thick layer of stereome adjoins the leptome, decreasing to one or two cell layers on the hadrome side of the bundle; chloroplasts massed among the outer layers of the cortex, but occur throughout.

Sarracenia purpurea.—Well known for its insect-capturing pitchers. *Stem*: epidermis and first hypodermal layer thick-walled; lysigenic air cavities throughout pith and cortex; resin deposits confined to the epidermis and one or two hypodermal cell layers, but where wounded heavy deposits of resin take place in the exposed and underlying cells. *Root*: cell walls firm, resinous bodies present throughout, but especially prominent in the two outer cortical layers, in which the cell walls are also strongly thickened. *Leaf*: epidermis thick-walled and slightly cuticularized; stomata on both sides of the lamina, with guard cells strongly cuticularized and slightly protuberant; resinous deposits throughout; inner face of lamina with strong downward pointing bristles.

Oxycoccus macrocarpus.—*Stem*: pith thick-walled, with resinous bodies; a thick layer of broad-celled bast forms a complete cylinder within the epidermis. *Leaf*: margins revolute, upper epidermis without stomata, heavily cuticularized, radial walls thick, wavy; hypodermal collenchyma of two or three cell layers on leptome side

of midvein, one or two cell layers on the side of the hadrome, development of the stereome cells also smaller on hadrome side; palisade of two cell layers; lower epidermis covered with wax, especially at the stomata, guard cells slightly elevated. Mycorrhiza present in the larger roots, wanting in the hairlike branches, no root hairs.

Andromeda polifolia.—*Leaf*: margins revolute, upper epidermal cells thick-walled, radial walls undulate, no stomata; lower epidermis supplied with unicellular short stiff hairs, and covered with wax, stomata slightly protuberant, strongly cuticularized beneath midvein; palisade of three layers of long narrow cells; stereome strongly developed above and below vascular bundle; on the ventral side this adjoining three layers of large thin-walled air cells and a one-layered hypoderma. *Root*: resinous deposits throughout, no mycorrhizal fungi found.

Chamaedaphne calyculata.—*Leaf*: margin slightly revolute, epidermis thick-walled, heavily cuticularized, cuticle rough, no stomata on upper surface; ventral epidermis covered by shield-shaped multicellular hairs, and a deposit of wax; cuticle unusually thickened beneath the midvein, guard cells sunken, subsidiary cells protuberant; palisade tissue of four or five layers. *Root*: inner and radial walls thickened, cortical tissues thick-walled; resin deposits in vascular bundle and cortex; no mycorrhizal fungi found.

Chiogenes hispidula.—*Leaf*: margin revolute, epidermal walls very thick, cuticle present, papillate, palisade not strongly developed; mesophyll cells in part thick-walled and in part thin-walled; resinous bodies in the epidermis; stomata slightly protuberant. *Stem*: resin present in cortex; mycorrhizal fungi in the epidermis of the smaller roots and throughout the cortex of the larger.

Vaccinium corymbosum.—*Leaf*: cuticle present, epidermal walls not thickened, palisade of one layer, mesophyll tissues with resinous bodies, cuticle of ventral surface papillate; abundant unicellular hairs on lower epidermis few on upper; leptome side of midvein adjoined by three layers of stereome and two or three layers of hypodermal collenchyma, on the hadrome side reduced to two of stereome and two of collenchyma, cuticular papilli usually developed beneath the midvein and at edge of leaf. *Root*: cortical tissue with resin, mycorrhiza present. No resin deposits found in stem.

Salix sericea.—*Leaf*: upper epidermal cells small, strongly cuticularized; mesophyll compact, palisade of two layers of long narrow cells; stomata on under surface, guard cells sunken beneath the slightly protuberant companion cells; hypoderma of five- or six-cell layers on hadrome side, and eight layers on leptome side of midvein. *Root*: resinous bodies present in medullary rays and cortex, the latter consisting of thick-walled cells; no mycorrhiza.

Ledum groenlandicum.—*Leaf*: upper epidermis rugose, with scattered unicellular hairs, margins strongly revolute, cuticle present, cell walls thickened, the radial walls being broadly undulate; lower epidermis covered with a thick cuticle and a felt of long multicellular and short unicellular hairs, glandular hairs usually present near the small veins, stomata protuberant; palisade of three or four layers of broadly oblong cells; beneath vascular tissue of midvein and between the mestome bundles occur large air cells which may form lysigenic air cavities in the older leaves. *Root*: mycorrhizal.

Larix laricina.—*Leaf*: bifacial, deciduous; epidermis thick-walled, slightly cuticularized, guard cells sunken beneath the companion cells; palisade tissue developed toward the dorsal surface, two layers thick showing a radial tendency, stereome reduced to a few cells beneath the leptome; two resin ducts near edges of leaf. *Root*: composed of mycorrhiza, resinous deposits throughout, cortical tissues early destroyed by fungus. When grown in culture solutions and well aerated, normal roots with root hairs are produced.

Picea Mariana.—Plants in bogs are stunted. *Leaf*: epidermal cells thick-walled, cuticle present, guard cells sunk beneath the companion cells; mesophyll cells compact, of a more or less radial palisade type. *Root*: mycorrhizal, resin deposits throughout, cortical tissues destroyed by fungus. Normal roots are developed under culture conditions.

Pinus Strobus.—Plants very much stunted in the bogs, leaves shorter and thicker. *Leaf*, epidermal walls so greatly thickened that scarcely a lumen remains, beneath this a hypodermal layer of thick-walled cells; mesophyll cells compact and of the usual lobate type. *Root*: mycorrhizal, cortical tissues traversed by the fungus hyphae; resinous deposits throughout. *Stem*: annual rings narrow

and distorted, resin bodies throughout cortex and meristematic tissues of the wood.

To summarize these characteristics, it is evident (1) that epidermal and hypodermal tissues are thick-walled; (2) that for the conservation of water these are reinforced outwardly by a heavy cuticle, by coverings of wax and air containing hairs; (3) that resinous bodies are found in the roots and leaves of many of the plants; (4) that there is a general reduction in the size of the leaves, and that these are frequently revolute-margined; (5) that palisade tissue is quite uniformly developed; (6) that mycorrhizal fungi are present in the roots of most of the plants; (7) that, when compared with the xerophytes of dry sand plains (25, 6), they show a similarity in respect to the reduction in size of the foliage, in the development of external protective coverings of the sub-aerial parts, and in the presence of palisade tissues, but are very different in the matter of root development and character of root structures.

To account for the peculiarities of the bog vegetation various theories have been brought forward. KIHLMAN (28), in accounting for the xerophilous character of the plants of arctic swamps, which include several species common to American bogs, lays stress upon two factors: (1) the low temperature of the moist substratum, and (2) the presence of drying winds. The former influences the plants by decreasing the power of absorption, the latter increases the rate of transpiration. The plants of such habitats must therefore be protected against the loss of water by the subaerial parts.

SCHIMPER (44, p. 11) in classifying the natural habitats in which xerophytes occur mentions among others "peat bogs, because of the humous acids in the soil." On page 18 he says:

The xerophilous character of the vegetation of peat moors has hitherto been considered an incomprehensible anomaly, and yet the rich supply of humous acids in the soil furnishes a condition for its occurrence as comprehensible as it is necessary. The presence of Scotch pine and heather on both dry sand and on wet peat is thus not more remarkable than is that of *Ledum palustre*, *Vaccinium uliginosum*, and other peat-plants on the cold dry soil in the polar zones.

Further (p. 124) the statement occurs that "on the very acid humus of moors the vegetation assumes a decidedly xerophilous character, because the humous acids impede the absorption of water by the

roots." However, in describing the arctic vegetation (44, pp. 11, 715), he follows the suggestion of KIHLMAN, a conclusion to which he had come independently. GANONG (16) also accepts KIHLMAN's explanation for the xerophilous nature of the raised-bog flora of New Brunswick.

In the study of the structural adaptations of these plants and the causes of their occurrence in bog areas, several questions arise. Are these two factors, cold substratum and acidity, efficient causes of xerophily? Do they act, in the case of the bogs of this region, with sufficient strength to cause xerophilous modifications in the plants there found, or to permit the growth of only such forms as are xerophilous?

The last question may be answered from field observations. They indicate that most low-ground plants grow quite as well on the bog substratum as on the ordinary swamp soils, and that the swamp species of this vicinity may all be found at one place or another growing on bog soils. It would seem that here the bog substratum is no more efficient as a selective agent than are the swamp soils.

The only cases which have come under my observation in southern Michigan which will throw light upon the question of the effectiveness of the temperatures and acidity in the production of xerophilous adaptations is in the case of *Picea Mariana*⁷ and *Pinus Strobus*. These two plants both show reduced size of stem and leaf, in the Oxford bog, when compared with plants growing on the margin. But to what extent this may be due to sterility of the bog substratum rather than to temperature and acidity is indeterminate at this time.

EXPERIMENTS.

To answer the question of the efficiency of a cold substratum and soil acidity to produce xerophily, experiments have been in progress for approximately two years. The difficulties in the way of experimentation along these lines are numerous. The means for controlling soil temperatures in bodies of soil sufficiently large for experimentation with the larger bog plants are practically beyond the possibility of a university laboratory. When it is further realized

⁷ The so-called *P. brevifolia* Pk. This form is certainly no more deserving of a distinctive name than is the bog form of the white pine.

that the experiments should extend over a series of years in the case of the shrubby forms, the problem becomes still more complicated.

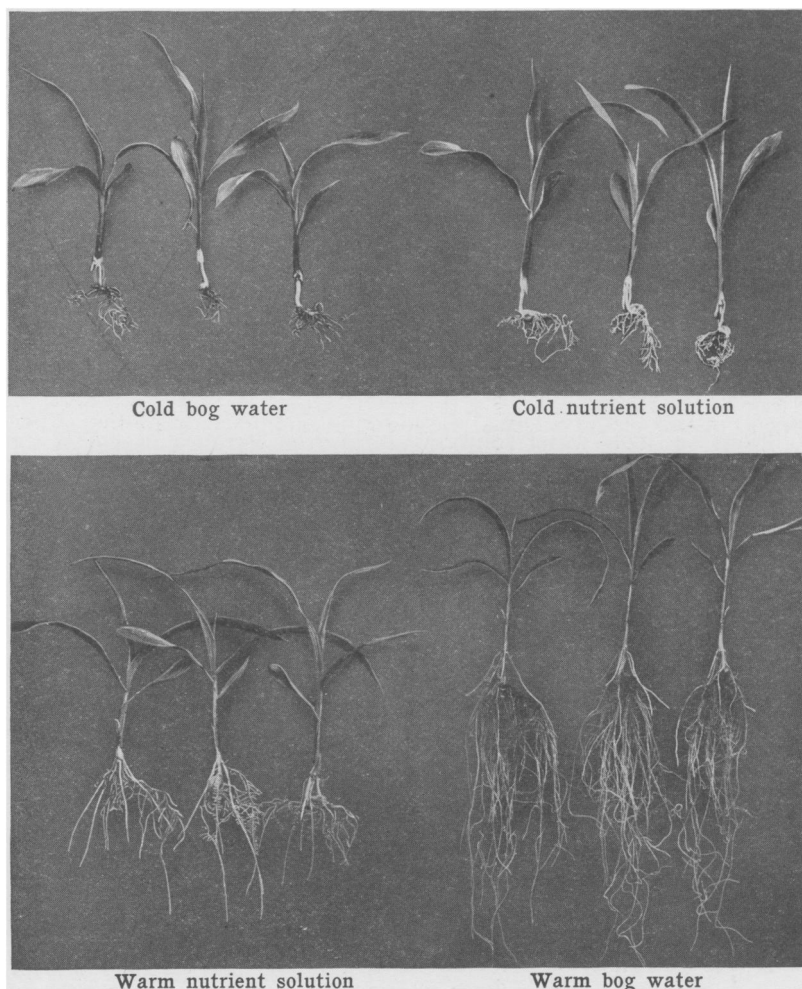


FIG. 12.—Average plants from the several cultures of Indian corn. From photographs.

In order to test the relative effects of humous acids (of the concentration found in the bogs of this vicinity) and low substratum temperatures, experiments were made in the form of water cultures

and with a peat substratum. All of the bog water used was brought to the plant house from the First Sister Lake. The acidity of the water varied from .0005 to .0023 normal acid, as measured by $n/100$ KOH solution.

WATER CULTURES.—(1) The plants were grown in four-liter battery jars covered with a plaster of Paris plate, having five one-inch openings for the passage of the plants and one of smaller size for a thermometer. Four such jars were employed in each experiment, two containing a 0.2 per cent. Knop's solution, and the others bog water. One of each was further maintained at a lower temperature. The cooling was accomplished by passing tap water through 15 feet of quarter-inch ($4.5^m \times 7^{mm}$) glass tubing, arranged in a coil within the jar, somewhat below the surface of the liquid. The sides and bottoms of the jars were covered with black paper, and those which were to be cooled were further surrounded by white paper and sphagnum. Daily readings of the temperatures of the air, warm-water solutions and cold-water solutions during the warmest period of the day were recorded. In this way the maximum differences between substrata and air were obtained. As these temperatures were not constant they exaggerate, to a slight degree, the average differences in temperature. Thus, four conditions were obtained which are comparable: (1) warm nutrient solution (temperature approximating that of the air of the plant-house), (2) warm bog solution, (3) cold nutrient solution, and (4) cold bog solution.

Fig. 12 shows the results of one of these experiments with corn. The photograph was taken eighteen days after the experiment was started. When the cultures were set up, the plumule had developed to a length of 2 inches (5^{cm}). The air temperatures during the period of experimentation averaged $18.8^\circ C.$, that of the warm cultures $18.7^\circ C.$, and of the cold cultures $10.8^\circ C.$

It is to be noted that under these conditions the best growth of the leaves and roots occurred in the bog water. But a reduction of 8° in the substratum temperatures caused a diminution in the development of both leaves and roots; the plants in the nutrient solution and the bog water being equally affected. When all of the plants had developed five leaves, it was noted that in the case of the cold cultures the two lower leaves had withered. This experiment was

repeated with corn, white lupine, and bean under similar conditions, with similar results. The greater development of roots in the case of the warm bog water may be due to the presence of a poison in very minute quantities; but this I have been unable to prove.

(2) A third culture was then made in which five plants of corn were grown in each of the four water culture conditions, and in addition in four similar conditions, using a mixture of sphagnum and peat for the substratum. Wooden boxes 2 feet long, 1 foot wide and a half foot deep ($60 \times 30 \times 15^{\text{cm}}$) were constructed, and two were lined with galvanized iron. The bottoms of the unlined ones were perforated so as to allow of easy drainage. The lined boxes served for the undrained conditions. Further, in one of the drained and in one of the undrained boxes, 40 feet (12^{m}) of glass tubing, bent into coils, the joints being connected by rubber tubing, were arranged so that a constant flow of cold water, for lowering the temperature, could be maintained. The water level in the undrained bog substratum was kept just below the surface. The water was obtained from the bog at First Sister Lake, but occasionally all were watered with distilled water. The amount added to each box was practically the same. In order to keep the solutions in the water culture jars at the same acidity as in the undrained boxes, the water was siphoned off and transferred once a week. Care was taken in this transfer to aerate the water in the boxes as little as possible, while that of the jars was aerated at irregular intervals by means of a bulb. There were thus produced eight conditions, in which it was possible to test the effect of the acidity of the bog water, of aeration (drainage) of the substratum, and of low temperatures. As a result, it was found that the growth of roots and leaves was best in the warm bog water, in the warm nutrient solution, and in the drained warm peat substratum. Reduction in size of both roots and leaves occurred in the cold bog and nutrient solutions, and in the drained cold and undrained warm and cold peat substrata. But the plants in the undrained cold peat showed the most marked reduction in size. The conclusion was reached (1) that humous acids (acidity varying from .0005 to .0023 normal acid) have no effect upon corn in the matter of leaf and root development; (2) that low temperature and lack of aeration of the substratum both cause reduction in size;

and (3) that when low temperature is combined with poor aeration the effect is very marked.

This experiment was repeated with peas; and the same result was obtained, although the effects were not so marked (*fig. 13*). The roots in the undrained substrata were killed when they attained a depth of a half inch (12^{mm}) below the surface.

(3) In order to test the effects of drainage and of low temperature on bog species, another set of cultures in peat-sphagnum substrata was made. The apparatus used consisted of two flower-pots and two glass dishes approximately a foot in diameter and three inches

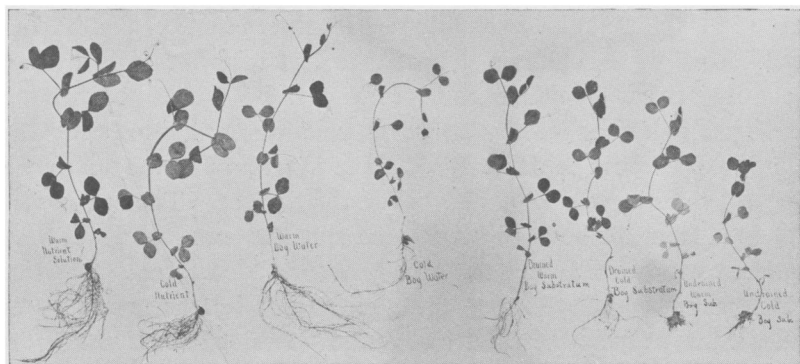


FIG. 13.—Effect of the several conditions upon the development of pea seedlings. All are average specimens. From photographs.

deep ($30 \times 7.5^{\text{cm}}$). A flower-pot and a glass dish were kept cool by passing cold water through fifteen feet of glass tubing arranged in coils, as in previous experiments. Three species were tested in these conditions: two-year-old *Larix laricina*, *Rumex acetosella*, and *Prunella vulgaris*. The first cultures were made in the spring of 1903 with the *Rumex* and *Prunella*. The air temperature averaged about eighteen degrees. The cold substratum was maintained about ten degrees lower. In the case of *Rumex* it was found that the largest leaves were produced in the drained peat-sphagnum substratum. Lack of drainage and low temperature both caused a reduction in leaf area, and when combined produced leaves which were less than half as large as those of the drained warm substratum.

The *Prunella* under the same conditions showed the same results.

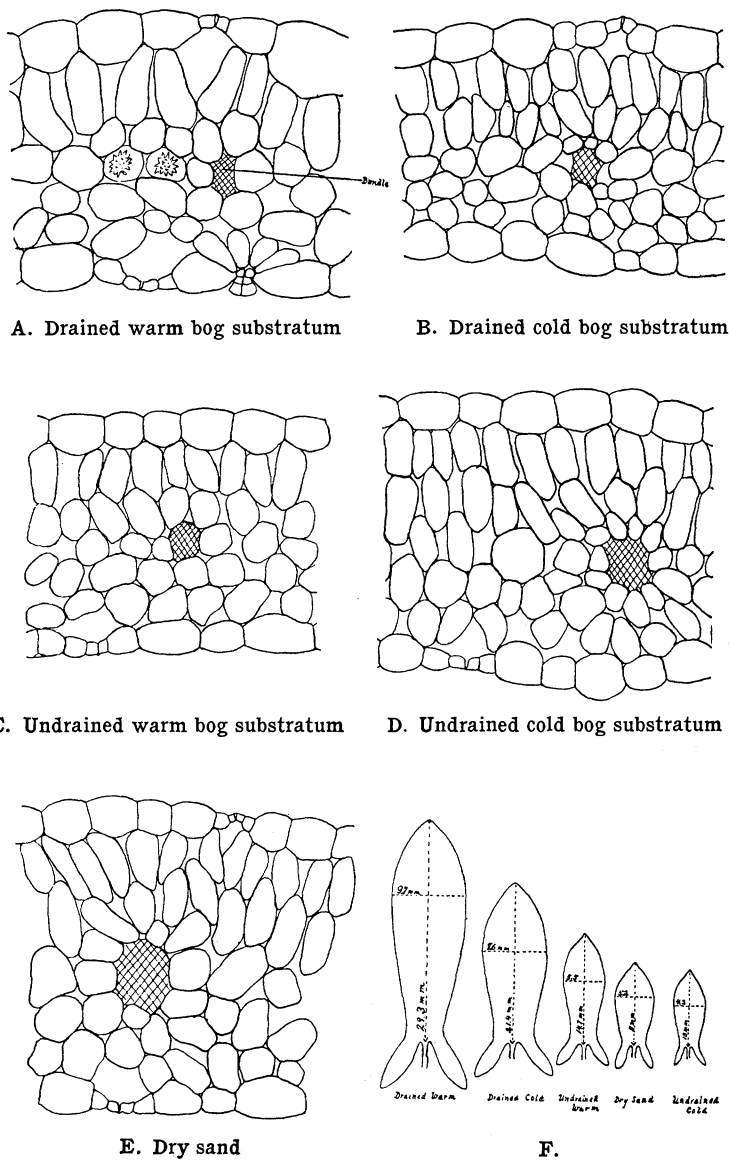


FIG. 14.—A, B, C, D, E, camera drawings of leaf sections resulting from cultures in the five conditions named. $\times 135$. F, diagrams showing average length and breadth of leaves.

Fifteen plants were grown in each condition. At the end of the experiment each had produced six to eight mature leaves. The leaves were measured as to length and breadth. An index was obtained by multiplying these two numbers together and averaging for each culture. Following are the indexes of leaf area thus derived: drained warm substratum 1268.3, drained cold 682.6, undrained warm 518.5, undrained cold 421.8.

In the spring of 1904 the experiment with *Rumex* was repeated. The results correspond with those of the preceding year. The structure of the leaves, resulting in the several cultures, was investigated, and found to show marked variations (56). *Fig. 14* represents the cross-sections and average leaf areas produced (seventy-five leaves being measured in each case). When grown on a warm drained substratum, the leaves are large, and the cells are exceedingly loose and turgid. The epidermis is composed of large thin-walled cells, having a thin cuticle outside. The mesophyll consists of a single layer of palisade and three layers of spongy tissue. No resin bodies are present. The plants grown in the undrained substratum, whose temperature was reduced about 8° C. below that of the air, show marked xerophilous characters. The leaf is reduced in area, increased in relative thickness, and the margins become revolute; the epidermal cells are smaller and outwardly thick-walled; a well-marked cuticle is present; the mesophyll is very compact and made up of two or three layers of well-developed palisade cells and three layers of spongy tissue; and in the epidermal cells and those adjacent to the bundles there are marked accumulations of resinous bodies.

For the purpose of comparison, a corresponding set of plants were grown on sand kept just sufficiently moist to allow the plants to live. As will be seen in *fig. 14*, the xerophily is not more marked than that of the undrained cold bog substratum. *Fig. 15* shows the relative appearance of the plants produced by the different conditions.

In the case of the plants grown in the undrained warm and the drained cold substrata, these same effects were noticeable, but to a less marked degree. That, in the case of the undrained cultures, these effects are not due to the acidity of the bog water is shown by

the fact that plants grown in bog-water cultures develop normally.

The light conditions in the several cultures were the same, direct sunlight being avoided by a cloth screen. It is evident that in this case there is no response to strong light in the development of the palisade tissue (49). It would seem rather to be a response called forth by a reduced transpiration current (44, p. 7). As to function, it may aid in the transfer of food materials as suggested by HABERLANDT (20, p. 260).



FIG. 15.—Average plants showing effect of surrounding conditions. From photographs.

This plant proved to be the most plastic of all of the species used in the experimentation, and was the only one which showed marked variation in the internal structures. Ecologically the results indicate (1) that an undrained peat substratum may cause xerophilous structures, but that the effect is to be correlated with lack of aeration of the substratum rather than with the acidity; (2) that the same effect may be induced by lowering the substratum temperature (the air temperature remaining the same), and thus impeding the rate of

root growth and absorption; (3) that a cold undrained bog substratum is analogous to a dry warm soil in that both produce physiological drought; (4) that resin bodies, which are characteristic of the bog plants, may be produced by this environment in a plant which under favorable conditions is without them.

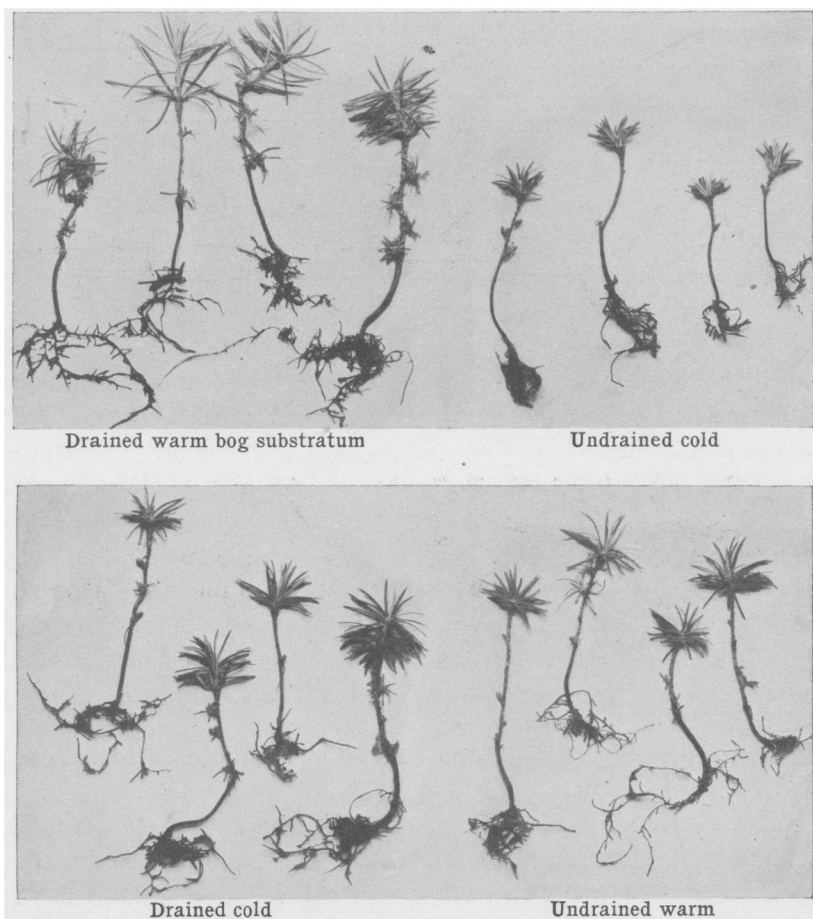


FIG. 16.—Relative effects of drainage and reduced substratum temperature, on *Larix*. From photographs.

The seedling tamaracks, ten of which were cultivated in each of the four conditions just described for the *Rumex*, also showed considerable variation. Their relative development at the end of forty-

four days is shown in *fig. 16*. The leaves of the drained warm substratum have an average length of 12.6 mm, of the drained cold 10 mm, of the undrained warm 11.4 mm, and of the undrained cold 6.3 mm. Internally, the leaves show a reduction in the intercellular spaces and in the size of the cells in the case of the plants grown on the undrained cold substratum, when compared with those of the warm drained condition.

(4) In another series of experiments with plants of *Larix* four to five years old practically the same results were obtained. There were the greatest number and length of leaves and branches produced in the case of the drained warm substratum. The smallest and shortest leaves and branches were produced by the undrained cold substratum.

Experiments with *Ledum Groenlandicum*, *Chamaedaphne calyculata*, *Andromeda Polifolia*, *Betula pumila*, and *Oxycoccus macrocarpus* have failed to produce satisfactory results. This is believed to be due to the shortness of the time under which they were under cultivation. The plants were brought from the bogs in the late autumn and placed in cold frames over the winter. About the beginning of March they were brought into the greenhouse, and after a few days planted in the warm and cold, drained and undrained boxes, previously described. They have grown vigorously, but the differences noticeable may not be correlated with the four conditions. The cranberry has shown the greatest amount of plasticity, but this could not in all cases be correlated with the environment. If these plants can be kept under known conditions for two or more years, it is probable that they will yield valuable results.

(5) In order to test the effect of mineral soils, and the ability to withstand the presence of large quantities of calcium and magnesium, specimens of andromeda, cassandra, and cranberry were grown in sandy loam and sand. They were watered daily with tap water. The cultures were started in the autumn of 1902, and produced vigorous vegetative shoots during the summer of 1903. They failed to bloom, however, and although they are growing well at this time (June 1904), they have again failed to bloom. This may be in part due to the warm plant-house conditions. The experiment was originally started to observe the changes in the roots, and in so far

have been of value. In a sphagnum substratum all three of the plants produced hairlike roots which attain a length of 5-7^{cm}. The roots are commonly several times branched, very little difference in thickness being shown by the several branches. When grown in sand the roots are still slender, but the frequency of branching is enormously increased. Usually the branching occurs just back of the growing tip. The older root ceases growth as the lateral root develops. The branch continues for 2-3^{mm}, and it also stops growth with the formation of a second lateral root. The result of this process is a zigzag root showing root branches which have been successively the main root tip. Occasionally several lateral roots develop and the main axis is divided.

(6) The statement that waters containing lime and other mineral salts are unfavorable to the growth of sphagnum has gained wide circulation in ecological literature. Because of the great abundance of lime and magnesia in the waters of this vicinity, I was led to test this fact by growing the sphagnum in tap water and solutions of CaCO_3 . In one experiment the water in a battery jar was saturated with CO_2 , CaCO_3 was added in excess, and the CO_2 was again allowed to pass through the water for thirty minutes. In this solution sphagnum was placed, and it has been growing vigorously for three months, although watered daily with water containing over 100 parts of CaCO_3 to the million. Some of the sphagnum cultures have been running for ten months, and show no signs of deterioration. Whether the sphagnum of this vicinity has become accustomed to the presence of lime, owing to the nature of the soil waters, or whether sphagnum is generally able to withstand such conditions, remains to be proved. Since the above experiments were performed, I have found an account of somewhat similar experiments by WEBER (58), the results of which are the same. It would seem, therefore, that the presence or absence of sphagnum is not to be correlated with the presence or absence of lime.

(7) Among the plants growing in the bogs of this vicinity the following have been found to possess mycorrhiza: *Larix laricina*, *Pinus Strobus*, *Picea Mariana*, *Betula lutea*, *Betula pumila*, *Oxycoccus macrocarpus*, *O. Oxycoccus*, *Chiogenes hispidula*, *Vaccinium corymbosum*, *Ledum Groenlandicum*, *Populus tremuloides*.

In order to get at the conditions which favor or cause the development of mycorrhiza, cultures of *Larix* were made in loose sphagnum, sand, undrained sphagnum, etc. The roots in the many other cultures previously noted were also carefully watched. It has been found without exception that where the plants were grown under properly aerated soil conditions, normal roots developed in place of the mycorrhiza. That the acidity of the bog water has nothing to do with the production of mycorrhiza is shown by the fact that in water cultures of the same acidity as the solution in the undrained peat, the plants develop normal roots. In the case of roots developed in loose sphagnum, sand, and moist air, an abundance of root hairs were produced. The normal roots in *Larix* have a diameter about three times that of the mycorrhiza, so that when they begin to develop they appear like white pendants from the dark brown mycorrhiza. That mycorrhiza will not develop in a well-aerated substratum was further tested by the following experiment: Two 30^{cm} test tubes were set upright, and 8^{cm} of glass beads were poured into the bottom of each. Into one a glass tube, at whose end were several small openings, was passed to the bottom. The upper part of the tube was connected with a gasometer. Upon this foundation of beads, three plants of *Larix* were planted in a 5^{cm} layer of peat in each tube. The water level in the two tubes was kept just at the surface, bog water being used throughout. Air was then forced from the gasometer to the bottom of the one tube and allowed to pass slowly through the beads and peat. When the experiment was started, all of the plants possessed only mycorrhiza. In the course of a week the aerated plants began to develop normal roots. The experiment was continued for six weeks. The unaerated plants developed only mycorrhiza, while those which were aerated developed normal roots.⁸ The growth of mycorrhiza is exceedingly slow, and the fungus grows with the root. The development of the above ground parts corresponds to the root development. The plants which produce normal roots have longer shoots, and longer, thicker leaves.

It seems evident, in the case of *Larix* at least, that (1) the mycorrhizas develop only in poorly aerated substrata; (2) their growth is

⁸ In the case of a number of the plants of *Larix* grown in the undrained peat in previous experiments, one or two normal roots were developed just at the surface of the substratum.

exceedingly slow, the fungus developing along with the root; (3) the acidity of the substratum is not a factor in their development; (4) in a naturally well-aerated soil or in an artificially aerated substratum normal roots develop; (5) when the roots are not surrounded by water, root hairs develop abundantly. Mycorrhiza therefore appears to be an abnormal root condition. Whether the fungus is of advantage to the root under these poorly aerated conditions cannot as yet be stated.

(8) In order to determine whether the zone of tamaracks follows the shrub zone because of the occasional submergence of the sedge zone, the following test was made: Ten *Larix* seedlings averaging 7^{cm} in height were placed in a crystallizing dish with the roots imbedded in 2^{cm} of sphagnum. Over this a layer of bog water 4^{cm} in depth was maintained for six weeks. The plants grew quite as well as those in a peat substratum. Stem and root submergence is therefore not a factor in preventing the growth of seedlings tamarack in the sedge zone. The liability to submergence in the bogs I have studied would not extend over nearly so long a period of time.

V. Summary.

The Huron River basin shows three well-marked physiographic divisions which differ in forest covering and the possibilities for bog development. These are (1) the region of the Saginaw-Erie interlobate moraine; (2) the Erie morainic belt; and (3) the lake plain.

In discussing the meteorological conditions of a region as affecting the flora, attention is called to the fact that the significance of the data is not apparent unless the temperature and rainfall phenomena are compared with those of the optimum region of dispersal of the plant societies involved. In the case of the bog plant societies the temperature of the region under discussion averages several degrees higher during the summer months than the eastern maritime provinces of Canada (the optimum region of dispersal for the bog plants), while the rainfall during the same period averages about three-fourths as much. This is believed to account for the general difference in character and development of bog societies in the two regions.

Bog and lake basins are here associated with deposits of glacial drift. The most frequent causes of these basins are (1) the melt-

ing of stagnant bodies of ice in old glacial drainage channels after their abandonment; (2) the differential settling of fluvio-glacial deposits; and (3) unequal deposition of glacial material in moraines and till plains.

Marl and peat deposits are commonly associated. The former are of interest in so far as they aid in the filling of the lake basins. Both are formed through plant agencies.

Peat deposits may be classified under two general heads: (1) those connected with glaciation, and (2) those associated with coastal plain phenomena. In North America the bulk of the deposits come under the first head. Their geographic distribution approximates that of the Pleistocene glaciers. Near the southern border the peat areas are scattered, but they become more nearly continuous and more independent of depressions as we go northward. The same effect is brought about in mountainous regions by increased altitude. In the tundra, peat accumulates because of the low temperature and in spite of the scant vegetation. In temperate regions a vigorous vegetation and areas of stagnant water render peat accumulation possible. In the southern coastal plain swamps, peat is formed in stagnant water because of the luxuriant vegetation and in spite of the high temperature.

During peat formation two processes are involved: (1) *eremacausis* and (2) *putrefaction*. The former is essentially an oxidizing process, brought about in the presence of air by certain fungi and bacteria. Its products are of direct value as food materials for plants. Putrefaction is carried on in the absence of oxygen and is essentially reduction; the organisms involved are anaerobic bacteria, and the products are of no value to the higher plants as food materials. The accumulation of peat depends upon the scarcity of oxygen below the water level, the acidity of the ground water, and the occurrence of low temperatures.

Peat varies in color beneath the various plant societies, being light brown in the youngest (bog sedge) and dark brown in the oldest, the darkest and most thoroughly decayed form being known as "muck." As disintegration proceeds it brings about a decrease in water capacity, a decrease in volatile combustible matter, and an increase in the amount of ash.

The bog as a habitat for plants differs widely from the other plant habitats of the region in that its substratum has been built by fore-runners of the present vegetation. Owing to the influence of the wind in the production of waves, the bogs are largely wanting on the eastern shores of lakes, and in the case of basins which have been almost completely filled with peat, the open water lies toward the eastern margin.

It is well known that bog areas are more liable to late spring frosts than adjoining uplands. This is due to the topography as it affects air drainage, and to the low conductivity of the substratum covering. Under natural conditions it has been found that the areas of cassandra and tamarack dominance are more exposed to late frosts than other societies.

Observations in bog areas show that the soil temperatures beneath the several plant societies differ markedly in range. The records indicate that the areas of bog sedges have temperatures corresponding closely with those of the upland and approximating those of the atmosphere. The willow-sedge (swamp) and maple-poplar areas have slightly lower temperatures during early spring. When the trees leaf out, however, the shade produced causes the maple-poplar area to have the lowest temperatures recorded. The bog shrub and tamarack societies show the lowest average temperature throughout the spring months.

Low soil temperatures retard chemical action, diffusion, solution, and osmosis, and render the substratum unsuited to soil bacteria. When coincident with higher air temperatures, plants having a low transpiration ratio are favored in the competition between species.

In so far as southern Michigan is concerned, the substratum temperatures prevailing in bog areas do not seem to be adequate to account for the presence or absence of bog plants or their xerophilous structures. Experiments suggest, however, that farther north this factor is of prime importance.

In texture the bog substratum shows every gradation from the coarse fibrous peat of the bog-sedge zone to the black powdery muck of cleared land. Bog soils in general do not afford as good a foothold for trees as do the mineral soils.

Peat is very resistant to the diffusion of mineral salts, hence bog

areas have a very different soil solution from that of the mineral soils adjoining. The high water capacity of peat is detrimental to plants, in so far as it prevents proper aeration of the substratum. Bog waters have no higher osmotic pressure than ordinary soil waters.

The absence of sphagnum from local bogs cannot be explained by the presence of calcium salts, as shown by observation, chemical analyses, and experiments.

The acidity of local bog water varies from .00015 to .00258 normal acid. The lowest values are found in areas covered by bog sedges and swamp plants, and they are approximately the same. The highest occur under the tamaracks. The variations in acidity are related inversely to the temperature. As shown by experiment, this is because of increased oxidation at the higher temperatures. It is suggested that we should find increased acidity as we go north. There is no apparent relation between color and acidity, except that light colored waters usually show slight acidity. The acid nature of the soil solution is a factor in the competition between different species for the occupancy of bog areas.

Bog soils are notably deficient in potassium and available nitrogen. Nitrifying bacteria are prevented from carrying on their normal activities by the acidity of the soil solution, by the lack of oxygen, and by the lower temperature of the substratum.

With few exceptions bog plants are light-demanding forms; hence, in their competition with one another, size and shading ability are prime factors.

That the conditions in the Huron valley are at present not as favorable to the bog plants as to the swamp plants, is shown wherever the two societies come into competition. This fact must be contrasted with the situation in the optimum region of the distribution of bog plants, where the opposite relation has been shown to exist.

An examination of all the physical and chemical data now available fails to account for the differences in flora of bog and swamp areas in this region. The most important factor is believed to be their physiographic history. Where the habitat dates back to Pleistocene times and has remained undisturbed, we find today the bog flora. Where the habitat is of recent origin or has been recently dis-

turbed, we find the swamp flora, or mixtures of swamp and bog species.

The nature of the bog plant societies of the Huron basin is shown by the description of several local bogs, selected to show both the local bog flora and the variation in societies, and arranged to present the genetic changes in a bog flora as a basin filled by peat accumulation. It is shown that during the early stages of bog development, bog sedge, bog shrub, and conifer societies follow each other in the invasion of the basin. These several societies may vary considerably in composition, but they are closely related and show every gradation in a definite order of succession. The bog conifers, however, show no relationship to the surrounding broad-leaved forests of the upland. On the other hand, where clearing has occurred, swamp sedges, swamp shrubs, and swamp trees gain the ascendancy, and these not only show an order of succession among themselves, but are genetically related to the broad-leaved trees of the region. The bog societies are part of the northeastern conifer forest formation, while the swamp societies are related to the southeastern broad-leaved forests.

An anatomical study of the bog plants shows that epidermal and hypodermal tissues are thick-walled, that a heavy cuticle is present, frequently supplemented by wax and hairs. Resinous bodies are to be found in the roots and leaves of many of the plants. The leaves are usually small and revolute-margined. Palisade tissue makes up a large part of the mesophyll. Mycorrhizas are present in most of the plants. Bog plants resemble the plants of dry sand plains in reduction of foliage area, in development of protective coverings for above-ground parts, and in palisade tissues, but differ from the latter in the matter of root development and root structures.

Experiments indicate that the local bog water itself has no tendency toward the production of xerophilous modifications. Low soil temperatures and lack of soil aeration, however, cause a reduction in the development of the several plant organs. When these two factors are combined, the effect is very marked.

Experiments with *Rumex acetosella* are of especial interest in that nearly all of the characteristics of bog plants may be developed either by lowering the soil temperature, as compared with the air temperature, by preventing proper soil aeration, or by growing in

dry sand. Palisade tissue was developed in the leaves of these plants in diffuse light, and it is shown that palisade tissue is to be correlated with physiological drought. An analogy between the bog habitat and the dry sand habitat is established.

Experiments with *Larix* indicate that mycorrhizas develop only in poorly aerated substrata; their growth is exceedingly slow; the acidity of the substratum is not a factor in their development; a naturally or artificially aerated substratum favors the development of normal roots, and these roots when not surrounded by water develop root hairs abundantly. *Larix* seedlings can withstand prolonged submergence. When exposed to low substratum temperatures and poorly aerated soil conditions, *Larix* produces more xerophilous leaves.

Further field work on the bog plant societies needs to be carried on in the region extending from Winnipeg to New Brunswick. Data on the soil and air temperatures, the acidity, the chemical composition of the soil solution, and the plants associated in bog areas throughout this region will go far toward solving the problems of the distribution of bog plants. Experimentation on the production of xerophilous structures by bog conditions should be continued on a larger scale than is possible in the ordinary university plant-house.

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